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STUDIES OF THE FOOD HABITS AND THE HABITAT OF MOOSE IN ONTARIO

By

Randolph L. Peterson

TORONTO
MAY 30, 1953

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STUDIES OF THE FOOD HABITS AND THE HABITAT OF MOOSE IN ONTARIO

by

RANDOLPH L. PETERSON

INTRODUCTION

THE MOOSE is an integral part of the biotic communities of much of North America's northern forests. The composition of the flora and fauna of these areas has a definite effect on moose populations, and the moose itself exerts considerable influence on the surrounding biotic association. In the present paper consideration will be limited to the inter-relations of the moose and the flora of its habitat. In the course of my original studies of moose (Peterson, 1949) of which the present paper constitutes a part, attempts were made to review many of the broader aspects of the general ecology, life history, habits and management of moose. It is hoped that treatments of these latter aspects may be published shortly.

No previous ecological studies of moose have been carried out in Ontario and only limited data are yet available from that region to the east of this province. The works of Murie (1934), Aldous and Krefting (1946), Hosley (1949) and Krefting (1951) on Isle Royale in Michigan have provided the first detailed data on the ecology of moose in eastern North America. In many respects my own research in Ontario has been supplementary to these Isle Royale studies. It has therefore seemed desirable to review the results of these studies together with other scattered data concerning the moose in eastern North America.

Elsewhere (Peterson, 1950) I reviewed the general classification of the North American forms. Later (Peterson, 1952) I made more detailed studies of the circumpolar relationships of the genus *Alces* and have shown that both new and old world forms should be regarded as *Alces alces*. Moose of the region of Isle Royale and St. Ignace Island have been designated as *Alces alces andersoni* Peterson while animals from the Algonquin Provincial Park and eastward are regarded as *A. a. americana* (Clinton).

In Ontario, the most intensive field research has been carried out in Algonquin Provincial Park, which may be regarded as

characteristic of the so-called Canadian biotic province of Dice (1943) and on St. Ignace and adjacent islands along the north shore of Lake Superior (fig. 1) which are Hudsonian in character.

Work in Algonquin Provincial Park was largely restricted to five townships, the east half of Butt and most of Devine, Bishop, Hunter and McLaughlin, or an area of approximately 275 square miles.

St. Ignace with its adjacent small islands constitutes approximately 110 square miles. Simpson Island adds roughly thirty square miles, to provide a study area of about 140 square miles. All of these islands have been logged rather recently for pulpwood, where suitable stands could be found. Two small areas were burned over in 1936: One on St. Ignace Island, and one on Simpson Island.

No thorough biological research has hitherto been carried out on these islands. Agassiz and Cabot (1850) apparently visited St. Ignace in 1848. They collected a few plants and commented on the fauna but did not see moose. Apparently woodland caribou was the major big game animal present at that time. They tell of an Indian having killed twenty-five caribou on St. Ignace Island the previous winter. According to local residents of Rossport, the moose first appeared on these islands about 1905. Shiras (1935) visited this area in 1917 and found an abundant population of moose. He describes seeing 150 animals during one trip and photographed many. He found that moose had so completely denuded the islands of available food that he suggests they must surely cross to the mainland in the winter to avoid starvation. He remarks on the absence of calves, having seen only one, and suggests that this scarcity was correlated with the depleted food supply. He saw tracks of caribou but saw no signs of white-tailed deer on the island, although he remarks that they were common on the mainland.

In 1947 and 1948 the moose population was found to be quite high on these islands, but caribou were extremely rare. White-tailed deer are now resident, although their numbers were comparatively low in both years. Black bear and timber wolves were observed and their signs seemed plentiful. The avian and mammalian fauna appeared typically Hudsonian—similar to mainland conditions except that the following species were noticeably absent: Skunk, woodchuck, porcupine, chipmunks and jumping mice.

In order to compare and contrast the results of work on St. Ignace with the important moose studies conducted on Isle

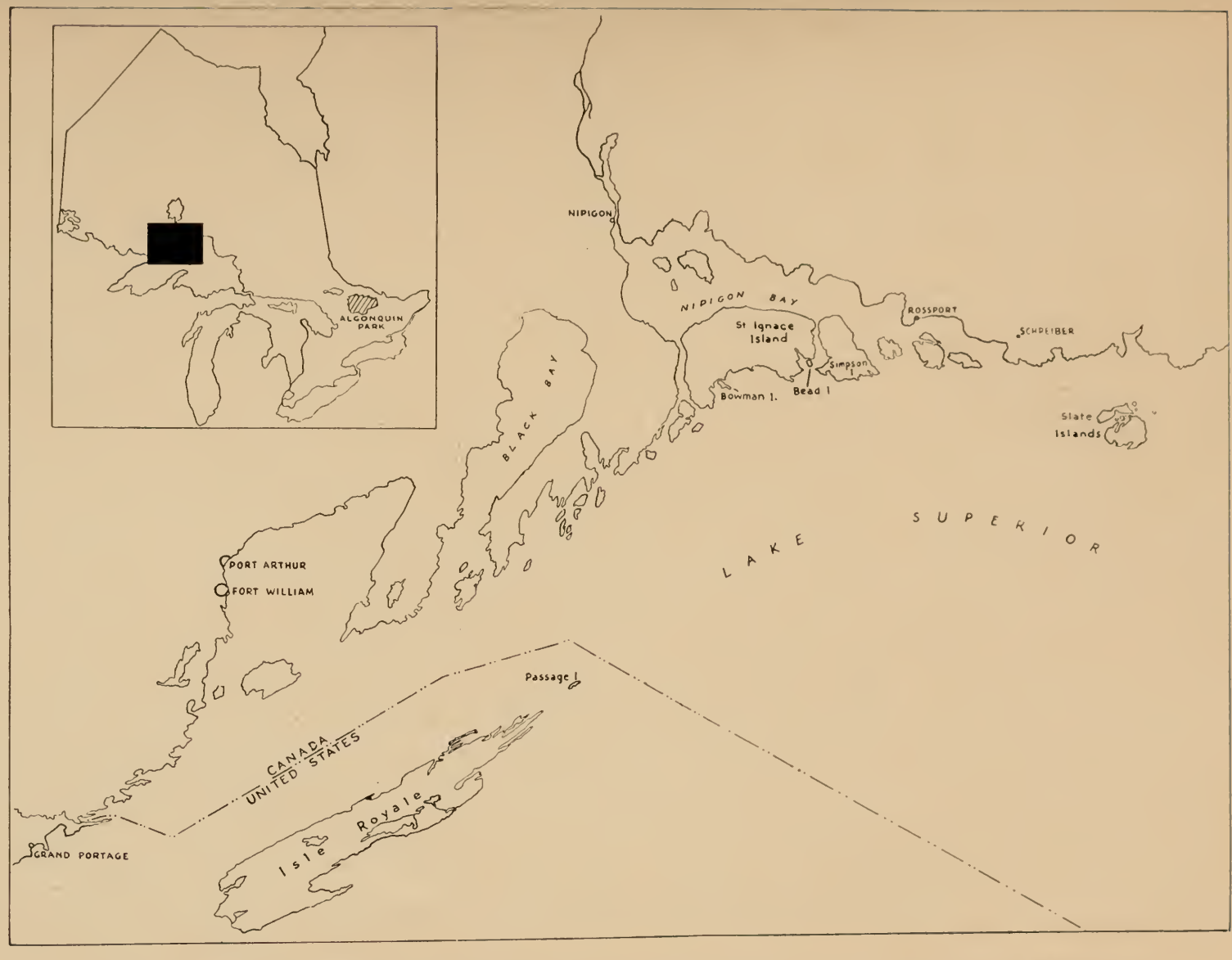

FIG. 1. Map of the north shore of Lake Superior showing the location of Isle Royale, Michigan and the St. Ignace Island study area, Ontario.

Royale (op. cit.) a brief visit was made in May, 1948. Isle Royale National Park lies about fifty miles southwest of St. Ignace Island (fig. 1).

The flora of the two areas are comparable except for a slight Canadian influence found on Isle Royale, as exemplified by limited local stands of sugar maple and a few yellow birch. Other species reported from Isle Royale which are apparently absent from St. Ignace Island include sumac (*Rhus glabra*), red oak (*Quercus borealis*), red maple (*Acer rubrum*), black ash (*Fraxinus nigra*) and green ash (*Fraxinus pennsylvanica lanceolata*).

Important ecological factors of Isle Royale which either serve as "controls" in studying conditions in the St. Ignace area or bear important relations to existing factors found there include the following: (1) Moose are restricted to Isle Royale, whereas they cross freely between the islands and mainland in the St. Ignace area. (2) No closely related competitor is present in Isle Royale, whereas both the while-tailed deer and caribou occur on the Canadian islands. (3) No active predator is found on Isle Royale, whereas both the black bear (which may prey on calves) and timber wolf are common on St. Ignace and Simpson Islands.

Acknowledgments

This study has been made possible by the generous cooperation and financial support of the Carling Conservation Club. The foresighted policy of undertaking a campaign directed toward the cause of wildlife research and conservation of natural resources and the proper appreciation of the necessity of continued research, on the part of representatives of the Carling Conservation Club, has greatly facilitated the progress of this and other research in Canada.

The Department of Lands and Forests of the Province of Ontario extended its fullest cooperation and provided many services through its administrative and field staff. Professor J. R. Dymond, former Director of the Royal Ontario Museum of Zoology, and now Head of the Department of Zoology, University of Toronto, gave much advice, cooperation and support in his capacity as supervisor of the original research project which formed the basis for this work. Mr. V. H. H. Williamson assisted in food studies during one season and carried out detailed examinations of moose stomach and dropping material in the Museum laboratory under a research grant from the

Research Council of Ontario. Mr. Thomas McCormick, Jr., provided many services as a guide and assistant during two seasons. Mr. Dalton Muir assisted in many ways while accompanying field activities to provide photographic records of our research. Mr. Lauritz W. Krefting, Regional Biologist, Fish and Wildlife Service, United States Department of the Interior, who has done much research concerning the Isle Royale moose population, kindly accompanied me on a brief inspection of that area and also provided many helpful suggestions, especially with reference to moose winter browse analysis. Dr. J. H. Soper of the Department of Botany, University of Toronto, kindly checked the identifications of many botanical specimens. Dr. M. L. Prebble, Officer-in-Charge of the Forest Insect Laboratory at Sault Ste. Marie, Ontario, kindly supplied information on the ecology, distribution and spread of the spruce budworm in Ontario. Dr. Walter P. Taylor kindly reviewed most of the manuscript and provided many helpful suggestions. Mrs. R. L. Peterson was a constant assistant in compiling data and preparing the original manuscript.

The entire staff of the Royal Ontario Museum of Zoology extended invaluable cooperation. Acknowledgments, with sincere thanks and appreciation, must be extended to a great number of other persons, too numerous to list here, who have assisted me in many ways in my studies of moose in Ontario.

Food Habit Studies

Food is a fundamental factor in the ecology of the moose. Winter is the season of greatest food scarcity. This, together with other adverse conditions at that time, makes late winter the most critical survival period for moose. For this reason special emphasis has been placed on a study of winter food habits.

The plants which are eaten do not provide the only basis for evaluating the importance of plant species in a moose habitat. Many important relationships involving food habits do not become apparent until each species is evaluated in terms of relative palatability, availability and actual percent of total food eaten.

A considerable quantity of available food is required to maintain a healthy moose population. Based on feeding experiments with caribou, reindeer and musk-ox, Palmer (1944) estimates that an air dry weight of 35 pounds of food daily is

required by adult moose in Alaska [presumably an average for all seasons]. Kellum (1941) conducted feeding experiments with captive moose in Michigan and found that when provided 200 pounds daily they actually consumed 40 to 50 pounds in winter and 50 to 60 pounds in summer. These weights were not dry weights and the greater poundage consumed in summer was thought probably to be the result of a higher water content in the green foods, although it was also considered by Kellum that moose actually eat more during summer while they are putting on considerable weight.

Methods

Several systems of browse analysis have been attempted by recent workers but most of them still leave much to be desired. They are either superficial and without statistical validity or they are so complicated and time-consuming that they become impracticable for most field problems. Aldous (1944) has worked out a deer browse survey method which appears to be most practicable for obtaining desired results. Aldous and Krefting (1946) applied this system to a moose browse survey on Isle Royale with apparent success. However, when this system has been applied elsewhere, difficulties were frequently encountered because of the presence of more than one species of browsing mammal. Even with this weakness, it has appeared to be the most practicable method available for certain areas, and since the deer and caribou populations of St. Ignace and adjacent islands were quite small, the Aldous system for moose browse analysis was applied there. In the application of the Aldous system certain statistical inaccuracies are encountered, but the desirability of comparing the results with those obtained on Isle Royale seemed to outweigh any need for attempting to modify the system for use in this study.

The Aldous browse survey method consists in sampling a given area to obtain the percentage occurrence of available food species and their degree of utilization. Only those species which are within reach or otherwise available to moose during the winter months are considered as available food. The sampling is carried out by surveying 1/100 acre plots at ten chain intervals. The plots are circular with a radius of 11.7 feet and are selected along surveyed transects which traverse all types of habitats and which are designed to give as true a representative sample as possible. Where transects are made along trails or roads the plots are placed well to one side to prevent obtaining

an excessively heavy browse situation created by constant browsing by animals traversing such trails.

Special tally sheets modified somewhat from that suggested by Aldous (1944) were used. On these the density and degree of browsing of each species are represented as a fraction (density/browsing). Mature trees with no available browse within reach of moose are disregarded by Aldous but have been included in this work as zero density in order to make the ecological appraisal of the general habitat more complete. In addition to the information suggested by Aldous a second column has been added for each plot in which the age classifications present are indicated by appropriate symbols.

Since it is impracticable to attempt absolute counts of individual species or of the exact amount of browsing that has taken place, a system of estimating these values is employed. For density of available browse, each species within each plot is classified as dominant, moderate, sparse or unavailable.

Density:
Dominant—D = 50-100% of plot covered with available browse.
Moderate—M = 10-50% of plot covered with available browse.
Sparse—S = trace to 10% of plot covered with available browse.
Unavailable—0 = species present but no browse available.

In classifying the degree of browsing the following nomenclature is employed:

Browsing:
Heavy—H = 50-100% of available browse consumed.
Moderate—M = 10-50% of available browse consumed.
Light—L = trace to 10% of available browse consumed.
Zero—0 = no browsing.

When recording these values in the tally sheet in the field, the letters are written as fractions and later transposed to numerical averages or entered directly using the following values:

D, H = 70% average (since 100% rarely exists, Aldous selected this average).
M, M = 30% average.
S, L = 5% average.
0, 0 = 0%.

After some practice this method of estimating percentages becomes quite simple and definite. When two different observers evaluated the same plot there were rarely any differences in the classifications arrived at.

TABLE I.—Summary of winter browse analysis of the St. Ignace Island Study area—1,000 plots, 1947-1948

Species available	1 Frequency of occurrence	2 Average density	3 Average degree browsing	4 % food eaten	5 % available
1. Balsam fir (*Abies balsamea*)	93	21.7	13.3	27.0	30.9
2. White birch (*Betula alba*)	74	5.7	22.3	12.0	8.2
3. Mountain ash (*Pyrus americana*)	57	3.1	32.8	9.4	4.4
4. R. o. dogwood (*Cornus stolonifera*)	23	2.3	44.2	9.4	3.3
5. Mountain maple (*Acer specatum*)	33	3.2	30.6	9.1	4.5
6. Highbush cranberry (*Viburnum Opulus*)	43	3.1	18.3	5.2	4.4
7. Mountain alder (*Almus crispa*)	19	2.5	19.0	4.5	3.7
8. Willows (*Salix* spp.)	15	1.0	46.1	4.2	1.4
9. Red-berried elder (*Sambucus racemosa*)	18	1.2	35.4	3.9	1.7
10. Juneberry (*Amelanchier* spp.)	31	1.8	32.6	2.6	
11. Speckled alder (*Alnus incana*)	16	4.0	7.3	2.7	5.6
12. Cherries (*Prunus* spp.)	9	.6	33.0	1.8	.8
13. Quaking aspen (*Populus tremuloides*)	22	.8	18.9	1.4	1.1
14. Raspberries (*Rubus* spp.)	23	3.2	4.2	1.2	4.6
15. Fly honeysuckles (*Lonicera* spp.)	8	.5	15.7	.8	.8
16. Balsam poplar (*Populus balsamifera*)	2	.3	26.8	.7	.3
17. Beaked hazelnut (*Corylus rostrata*)	1	.1	50.0	.7	.2
18. Roses (*Rosa* spp.)	20	1.2	6.0	.7	1.7
19. Ground hemlock (*Taxus canadensis*)	8	.5	13.2	.6	.7
20. Salmon berry (*Rubus parviflorus*)	2	.4	18.3	.5	.6
21. White cedar (*Thuja occidentalis*)	17	2.1	2.0	.4	3.0
22. Currants and gooseberries (*Ribes* spp.)	23	1.3	3.6	.4	1.9
23. White spruce (*Picea canadensis*)	49	4.8	.1	tr	6.9
24. Black spruce (*Picea mariana*)	37	4.6	tr	tr	6.6
25. Nine-bark (*Physocarpus opulifolius*)	tr	tr	tr	tr	tr
26. Tamarack (*Larix laricina*)	.2	.1	—	—	tr
27. Junipers (*Juniperus* spp.)	.1	tr	—	—	tr
28. Jack pine (*Pinus Banksiana*)	tr	tr	—	—	tr
29. White pine (*Pinus Strobus*)	tr	tr	—	—	tr

For a final analysis of these tally sheets to obtain relative values for any given area, the following type of breakdown is used (table I):

Frequency of occurrence—Column 1.
This is obtained by totalling the number of plots in which each species occurred and dividing this by the total number of plots analysed.
Average density—Column 2.
This figure is obtained by adding up the total density figures (numerators) for each species and dividing by the number of plots surveyed.
Average degree of browsing—Column 3.
Column three is obtained in a similar manner as column two except the degree of browsing figures (denominators) are totalled and divided by the number of plots in which each species occurred.
Percent of food eaten—Column 4.
For each species the average density (column 2) is multiplied by the average degree of browsing (column 3) to obtain a usage value. The percent of food eaten is obtained by dividing the usage value for a given species by the total of all usage values. The resulting figures represent the percent of total foods that each food species has contributed.
Percent of browse available—Column 5.
To represent the percent of total browse that each species provides the total of all average densities (column 2) is divided into each species' average density.

A total of 318 plots was completed in the spring and summer of 1947 on the St. Ignace Island area of Ontario. These were done while surveying transect lines with plane table and compass in order to obtain "fixes" on the uncharted inland lakes. In October, 1947, the islands were covered by Provincial Government aerial mappers, thus providing a complete series of aerial photographs. A set of these aerial photographs was obtained and used during 1948 in locating various "fixes" and in selecting transect lines which were measured by pacing. During May and June, 1948, 682 plots were analysed to give a total of 1,000 plots for the two years.

The most suitable season for carrying out browse analyses is during early spring, before the leaves appear. At this time it is much easier to appraise the results of the full winter's browsing without the confusing factors of new growth or considerable new spring or summer browsing.

To check on field browse analysis a series of moose stomachs was obtained and their contents analysed (table III).

A further check was made on the surprisingly high balsam utilization by analysing a large series of winter droppings (table IV). In these, conifer needles were found to be readily identifiable.

Feeding experiments were carried out in an effort to determine palatability preference of equally available species. This was done by placing the fresh cut branches of various species near a well-used "salt lick" and checking the order and degree of utilization by moose.

During work in Algonquin Provincial Park in 1946 it was found that the preponderance of deer made it impossible to use any suitable analysis system for quantitative estimates of

TABLE II.—Winter food of moose on S

Area	Summary 1947-1948		Summary 1947		Summary 1948		East St. Ignace	
Number of plots involved	1,000		318		682		261	
Species	Avail.	Diet	Avail.	Diet	Avail.	Diet	Avail.	Diet
1. Balsam fir	30.9	27.0	32.5	28.2	30.1	26.4	28.9	25.5
2. White birch	8.2	12.0	8.5	11.7	8.1	12.1	5.4	7.7
3. Mountain ash	4.4	9.4	4.2	7.4	4.5	10.3	3.7	8.5
4. R. o. dogwood	3.3	9.4	2.9	6.9	3.5	10.6	3.9	10.5
5. Mountain maple	4.5	9.1	5.6	9.3	4.0	9.0	7.2	13.7
6. Highbush cranberry	4.4	5.2	5.1	6.9	4.1	4.4	6.1	8.1
7. Mountain alder	3.7	4.5	3.5	4.8	3.8	4.4	6.4	4.3
8. Willow	1.4	4.2	1.2	3.0	1.5	4.8	1.5	4.2
9. R. b. elder	1.7	3.9	2.1	5.6	1.5	3.1	1.5	2.8
10. Juneberry	2.6	3.1	2.1	2.6	2.8	3.3	2.4	3.8
11. Sp. alder	5.6	2.7	6.3	4.2	5.3	2.0	5.0	2.1
12. Cherry	.8	1.8	1.3	2.0	.6	1.7	1.1	2.4
13. Q. aspen	1.1	1.4	1.0	1.0	1.1	1.6	.6	.5
14. Raspberry	4.6	1.2	5.1	1.3	4.4	1.2	6.6	1.1
15. F. honeysuckle	.8	.8	.7	.9	.8	.8	.9	1.1
16. Balsam poplar	.3	.7	.4	.5	.3	.8	.4	.5
17. Beaked hazelnut	.2	.7	.4	.7	.1	.7	.4	1.0
18. Rose	1.7	.7	1.9	1.1	1.6	.5	2.0	.7
19. Ground hemlock	.7	.6	.4	.2	.8	.8	.7	.6
20. Salmon berry	.6	.5	1.0	.9	.4	.3	.7	.4
21. White cedar	3.0	.4	1.2	.2	3.8	.5	1.8	.2
22. Currant and gooseberry	1.9	.4	1.3	.7	2.2	.3	1.2	.1
23. White spruce	6.9	tr	5.1	tr	7.7	tr	5.9	—
24. Black spruce	6.6	tr	6.0	tr	6.9	tr	5.4	—
25. Nine-bark	tr	tr	tr	tr	tr	tr	tr	tr
26. Tamarack	tr	—	tr	—	tr	—	.1	—
27. Juniper	tr	—	.1	—	tr	—	tr	—
28. Jack pine	tr	—	tr	—	tr	—	tr	—
29. White pine	tr	—	—	—	tr	—	tr	—

moose browse. Reliable qualitative data could be obtained only by direct observation of feeding animals, or by limiting the zone of consideration of browsed plants to that above six feet. (Deer rarely reach above six feet, while moose commonly feed on branches eight to ten feet above the ground, with occasional instances of 12 feet.) Other Algonquin field studies included special attention to aquatic food habits which were conducted by direct field observations of the animals as they actually fed.

nace and adjacent Islands, Ontario.

Cent. St. Ignace		West St. Ignace		Bowman Island		Bead Island		Simpson Island	
178		271		39		11		240	
Avail.	Diet	Avail.	Diet	Avail.	Diet	Avail.	Diet	Avail.	Diet
28.2	27.1	29.6	21.3	52.9	34.8	42.0	40.0	33.5	34.5
4.9	6.4	8.1	13.7	6.5	10.6	11.2	11.7	14.0	20.3
7.0	14.7	5.2	12.0	4.5	8.4	1.7	3.4	2.9	5.5
2.8	6.7	5.0	16.8	—	—	—	—	1.1	3.4
3.5	6.2	4.7	9.0	5.2	26.0	3.9	10.7	1.4	3.1
5.5	6.9	3.7	2.3	.7	2.2	2.6	6.7	2.7	2.9
2.7	5.0	3.0	5.1	.3	—	3.0	8.3	1.5	2.2
1.1	2.3	.8	3.2	—	—	—	—	2.5	8.8
1.8	5.9	1.2	3.1	1.0	3.7	3.9	10.7	2.3	4.7
4.8	3.8	3.2	3.7	3.4	2.6	—	—	.7	.7
6.9	3.9	6.5	.8	—	—	.4	tr	5.8	5.8
.5	1.0	.9	2.3	1.8	.4	—	—	.6	1.1
1.8	1.9	1.0	1.6	—	—	—	—	1.5	2.7
5.0	.6	3.1	.4	4.2	9.0	6.1	3.8	3.4	.7
1.0	1.0	.8	.3	—	—	—	—	.3	.5
.2	.2	.8	2.2	—	—	—	—	—	—
.5	2.3	tr	—	—	—	—	—	—	—
2.2	1.2	1.6	.4	.3	—	.8	tr	1.1	.6
.2	.4	1.1	.4	—	—	—	—	.6	1.3
1.1	1.8	.1	.3	—	—	—	—	.8	.2
2.9	.2	6.0	.5	—	—	—	—	1.3	.7
2.4	.5	1.7	.2	3.5	2.1	2.6	4.2	2.4	.8
7.7	—	5.1	.1	3.2	—	21.6	—	10.6	—
5.0	—	6.6	—	12.5	—	—	—	8.7	tr
tr	tr	—	—	—	—	—	—	—	—
tr	—	.3	—	—	—	—	—	tr	—
.2	—	—	—	—	—	—	—	tr	—
tr	—	tr	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—

TABLE III. Analysis of moose stomach contents.

Date	Locality Collected	Contents (percent volume)	
February 23, 1949	Twp. 11B, Chapleau Forest District, Ontario (hit by a truck)	Willow	59
		Jack Pine	40
		White birch	1
		Balsam fir	tr
March 10, 1949	Beaver River, Walls Twp. Kapuskasing Forest Dist. Ontario (diseased animal, purposely killed)	White cedar	64
		Balsam fir	35
		Willow	1
March 12, 1948	Murchison Is., Lake Nipigon Ontario (killed by wolves)	Balsam fir	100
March 12, 1950	Narrow L., Kenora Dist. Ontario	White birch	?
		Pin cherry	?
		Beaked hazelnut	?
March (early) 1947	Southern Champlain Twp. Kapuskasing Forest Dist., Ontario (killed by Indians)	Balsam fir	95
		Willow	3
		Beaked hazelnut	2
		Quaking aspen	tr
March (late) 1948	50 mi. NNW of Amos, Quebec (found dead)	Willow	50
		Balsam fir	40
		White birch	5
		Undetermined	5
April 3, 1948	Tashota, Ontario (illegally killed)	Balsam fir	97
		White birch	2
		Labrador tea	tr
April 12, 1950	Sioux Lookout, Ontario	Jack pine	93
		White birch	5
		Willow sp.	2
		Alder sp.	tr
April 1948	Geraldton, Ontario (killed by wolves)	Balsam fir	99
		White birch	tr
May 5, 1947	65 mi. SE of Kenora, Ontario	Balsam fir	74
		Willow	10
		Quaking aspen	10
		Beaked hazelnut	5
		Jack pine	tr
June 22, 1948	5 mi. N. of Jellico, Ontario (killed on highway by automobile)	Beaked hazelnut	40
		White birch	30
		Quaking aspen	15
		Pondweed	10
		White spruce Undetermined	5

TABLE III (*continued*).—Analysis of moose stomach contents.

Date	Locality Collected	Contents (percent volume)	
June 29, 1947	Ashmore Twp., Thunder Bay District, Ontario	Dwarf birch	60
		Willow	30
		Balsam fir, Bog bilberry, Undetermined	10
September 17, 1947	St. Ignace Island, Ontario (collected as specimen)	Quaking aspen	75
		White birch	25
October 15, 1947	Alsas, Gogama Forest Dist., Ontario (hunter killed)	Quaking aspen	40
		Willow	40
		Dwarf birch	15
		Ground hemlock	5
		White cedar	tr
October 19, 1947	Esher Twp., Chapleau Forest District, Ontario (hunter killed)	Willow, Bush honeysuckle, Balsam fir	50
		Undetermined (too finely digested)	50
October 21, 1947	Twp. 35, Chapleau Forest District, Ontario (hunter killed)	Balsam fir	95
		White birch, White cedar, Willow, Fern, Undetermined	5
October 25, 1947	Ghost River, Ontario (hunter killed)	Balsam fir	85
		Quaking aspen	5
		Speckled alder, R. o. dogwood, Willow, White cedar, White pine, Grass sp.	10
November 5, 1946	Denyes Twp., Chapleau Forest District, Ontario (hunter killed)	Balsam fir	98
		White cedar, Beaked hazelnut	2
November 12, 1948	Shobandowan River, Port Arthur Forest District, Ontario (diseased animal, purposely killed)	Balsam fir	95
		Leather leaf	3
		Willow	1
		Dogwood	tr
		Speckled alder	tr
		Raspberry	tr
November 14, 1947	Turtle Lake, Banfield Twp., North Bay Forest District, Ontario	Beaked hazelnut	50
		Balsam fir	35
		White birch	10
		Willow	5

TABLE III (*continued*)—Analysis of moose stomach contents.

Date	Locality Collected	Contents (percent valume)	
November 14, 1947	Honfield Twp., North Bay Forest District, Ontario	Maple sp.	40
		Balsam fir	30
		Willow	25
		Beaked hazelnut	5
		Quaking aspen	tr
November 20, 1947	Algonquin Provincial Park, Ontario	Balsam	98
		Beaked hazelnut	1
		Pin cherry	1
		White pine	tr
November (late) 1947	2½ mi. S. Oba, Ontario (fell through ice)	Balsam fir	45
		Quaking aspen	25
		Willow	15
		Juneberry	15
		White birch	tr
December 6, 1949	Red Lake, Kenora District, Ontario	Balsam fir	95
		Beaked hazelnut	2
		Pin cherry	2
		Undetermined	1
December 18, 1949	Sprucewood Forest Reserve, Manitoba	Pin cherry	35
		Beaked hazelnut	35
		Quaking aspen	25
		Prunus sp.	2
		Willow sp.	2
		Scotch pine	1
Winter 1947-1948	St. Ignace Is., Ontario (winter wolf kill)	Balsam fir	100

TABLE IV.—Occurrence of conifers in winter moose droppings.

Conifer species	Abundant occurrence	Moderate occurrence	Trace	Total occurrence
Date: 1945-46	Locality: Algonquin Provincial Park, Ontario. Sample: 425 pellets from 85 samples.			
Balsam fir	76%	23%	1%	100%
White cedar	5%	22%	69%	94%
Hemlock	28%	13%	51%	92
Date: 1946-47	Locality: St. Ignace and Simpson Islands, Ontario. Sample: 170 pellets from 34 samples.			
Balsam fir	85%	12%	3%	100%
White cedar	0%	21%	21%	42%
Black spruce	0%	0%	tr	tr
Date: 1947-48	Locality: St. Ignace and Simpson Islands, Ontario. Sample: 460 pellets from 92 samples.			
Balsam fir	99%	1%	0%	100%
White cedar	0%	9%	20%	29%
Ground hemlock	0%	1%	5%	6%

Seasonal Variation

Considerable seasonal variation is found both in the types of food eaten and in methods of feeding. Winter browsing is restricted to biting off the terminal twigs and branches of both coniferous and deciduous woody plants. Frequently limbs as large as one-half inch in diameter were found to have been bitten off by moose.

The habit of straddling and "riding down" small saplings during winter was found to be quite common in Algonquin Provincial Park, although few such instances of this were noted in the St. Ignace area. Probably this habit is more common in areas of scarce food supply. In Algonquin Park deer compete for many deciduous species and balsam fir has become greatly reduced through attacks by spruce budworms. Balsam saplings were most commonly found with tops broken off although some deciduous species showed similar injury.

In early spring moose appear to sample the majority of green species as they become available. The habit of chewing the bark from various species seems to reach its climax when the sap is rising, before the trees leaf out.

When trees, shrubs and various other plants are leafed out, moose commonly grasp the branches a foot or two from the terminal ends and with a sidewise motion of the head strip the leaves from the branches as they are pulled through the mouth. Utilization of woody plants continues throughout the year. The general palatability preferences seem to be similar to that of winter. Krefting (1946) has made a study of summer foods of moose on Isle Royale and found that 19 woody plant species were browsed and that 12 species formed an estimated 93 per cent of the summer diet.

Conifers are practically untouched from early spring to late fall and apparently moose do not return to feed on them until after the first of October, although Murie (1934) indicates that ground hemlock is utilized in both summer and winter, when available.

With the approach of spring, moose supplement the woody plant diet with herbaceous plants. Where available, aquatic and semi-aquatic plants form the more important bulk in this regard, although a great many upland herbs are sampled but few eaten in quantity.

Aquatic plants are sought long before most of them reach the surface and are utilized through the spring and summer, as long as the plants remain palatable. There was a noticeable decline

in aquatic feeding in Algonquin Provincial Park by the end of August, although moose were still feeding on pondweed (*Potamogeton*) in the St. Ignace area after the first of October. In the St. Ignace area bush honeysuckle (*Diervilla lonicera*) and large-leaved aster (*Aster macrophyllus*) appeared to be the most important small upland species.

Moose were observed to taste or graze lightly on several species of grass but nowhere was there any indication of serious feeding. McDowell and Moy (1942) found that moose of Montana fed on a great variety of grasses and estimated that they formed as high as 12 per cent of the diet in June. Observations in Ontario would indicate that grasses probably provide less than one per cent of the summer food in the east.

No attempt will be made to provide a list of the upland herbaceous species observed to be utilized by moose. A great many of these have been recorded by Murie (1934) and Hosley (1949).

Feeding on bark

Although the habit of chewing the bark from various trees is carried on from fall to spring, the great majority of instances noted in the St. Ignace area were in late winter or early spring. A few fresh aspen poles were used in construction of an enclosure in September, 1947. On February 22 we found that moose had chewed small portions of bark from two or three of the poles. Kellum (1941) found that captive moose would eat bark from fresh cut trunks all through the winter, although he agreed that it was preferred during spring. Quaking aspen was found to be the species most commonly "barked" on St. Ignace. A great majority of freshly fallen, wind-blown trees showed at least some signs of having been barked by moose. Standing aspens were occasionally barked. Trunks of both quaking aspen and balsam poplars, left near the salt lick in feeding experiments, were almost stripped clean in late May, although quaking aspen was more thoroughly utilized than balsam poplar. The former was rolled over so that it was cleaned of bark on all sides. Kellum (1941) reports that captive moose would kneel down to reach such logs, but we failed to observe this habit at St. Ignace.

Mountain ash was found to be most consistently barked, although mature trees were so scarce that it does not constitute an important source of this type of food in the St. Ignace area. In Algonquin Provincial Park various species of maples were

occasionally barked; however, red maple seemed to be the choice species. A few indications of moose having chewed the bark from balsam fir were noted in both study areas.

Murie (1934) concluded that moose feed on bark by preference during spring, but suggested that winter barking might be an indication of food shortage. These conclusions seem to be borne out by Ontario studies, although it seems doubtful that the small amount of winter barking observed would necessarily indicate food shortage.

Aquatic food habits

The characteristic habit of feeding on submerged and floating aquatic vegetation has led to a few apparently erroneous conclusions concerning moose. Many have associated the aquatic activity of moose with an attempt to escape pestiferous insects. Others have commonly reported that the chief aquatic food was the roots of water lilies. No evidence was found in Ontario studies to support either theory. In Algonquin Provincial Park many roots were found floating in the vicinity where moose commonly fed, yet none showed signs of having been fed on by moose. This observation is in contrast to the following statement made by Cahn (1937, p. 29): "In a puddle near Camel Lake [Quetico Provincial Park, Ontario] I found the moose pulling up and eating the succulent root system of these plants, and hundreds of huge half-eaten roots were floating on the surface." It appears that moose may, on occasion, consume parts of roots as well as stems and leaves of water lilies. Most of the roots found floating were pulled free of the bottom by moose while feeding on the stems and leaves.

In Algonquin Provincial Park there is such a great variety and abundance of aquatic vegetation that the present moose population has little noticeable effect on the general species composition and abundance. In the St. Ignace area only one aquatic species, pondweed (chiefly *Potamogeton Richardsonii*), provides the great bulk of available food. Other species, which are extremely rare in the area, include the common yellow pond lily (*Nymphaea advena*), eel grass (*Vallisneria spiralis*) and various members of the family Haloragidaceae including *Hippuris vulgaris*. Murie (1934) and Aldous and Krefting (1946) found that the supply of aquatic vegetation was quite low and concluded that the past high moose populations had been responsible for a great reduction from former years. Unfortunately there is no available record of the former abun-

dance of aquatic species of the St. Ignace area, but it seems likely that it may have been affected in a manner similar to that on Isle Royale, which might account for the scarcity of such forms as water lilies.

The relative proportion of aquatic plants in the spring and summer diet of the moose is unknown. McDowell and Moy (1942) have estimated that they provide only 2 to 5 per cent of the diet from June to October in Montana.

The summer diet of the moose in eastern North America consists of a much greater percentage of aquatic plants than is indicated for Montana. On several occasions animals were observed to feed on various aquatic plants for over an hour at a time, and in some instances over two hours.

In Algonquin Provincial Park, where a greater variety and abundance of aquatic species are found, we noticed that moose frequently selected a variety of species during one feeding period. There the most important food species included the common yellow pond lily (*Nymphaea advena*), water shield (*Brasenia Schreberi*), sweet-scented water lily (*Castalia odorata*), eel grass (*Vallisneria spiralis*), bur-reed (*Sparganium fluctuans*) and pondweed (*Potamogeton* spp.).

Horsetail (*Equisetum* spp.) was found in great abundance in Algonquin Provincial Park but was only occasionally browsed by moose. In the Chapleau district of Ontario we found extensive stands of this species that had been closely cropped by moose during July and August, 1946.

Wild rice (*Zizania*) was not observed in the Ontario study areas, although it is commonly reported to be fed on by moose when available (Oberholtzer, 1911, and others).

Other less important species observed to be utilized in Ontario include the following: *Sagittaria*, *Eleocharis*, *Scirpus subterminalis*, *Carex*, *Pontederia cordata*, *Juncus* and *Nymphaea microphylla*.

During June and early July the maximum utilization of common yellow pond lily and eel grass appeared to be reached in Algonquin Provincial Park. By the middle of July, water shield was found to be providing the great bulk of aquatic food.

A definite decline in the amount of aquatic feeding, observed in Algonquin Provincial Park during the latter part of August, seemed to be correlated with a reduction in palatability. By this time most forms had reached maturity and were becoming tough and soured. In the slow-moving streams and

shallow lakes most of the plants had acquired a coating of slime and other debris. Further reduction in palatability of water lilies was apparently caused by the attack of the larva of a chrysomelid beetle (*Donacia*). A similar, but less intensive, infestation was noted in the Chapleau district in August, 1946.

In the shallow waters of Algonquin Provincial Park, moose were not forced to dive to reach ample food. In early spring most animals merely submerged their heads to feed on the young growing plants. By mid-summer we noticed that moose rarely reached deeper than about 12 inches, with most animals feeding directly from the surface on floating leaves and stems. In the St. Ignace area moose were observed to feed in water at least 18 feet deep.

The water of Lake Superior is much colder than in the inland lakes and remains clear and free of debris. The earliest aquatic feeding noted on the inland lakes of St. Ignace Island was on June 4. This preceded any observed feeding in channels of Lake Superior proper by at least one month in 1947. It is not known how long aquatic feeding continued on the inland lakes in the St. Ignace area but moose were still feeding on *Potamogeton* in Lake Superior waters after the first of October.

Mineral springs

Mineral springs or so-called "salt licks" are utilized by moose wherever they occur. Such areas are usually seeping springs which are normally so thoroughly tramped by constant visits by animals that they appear little more than mud holes with a bit of standing water.

Cowan and Brink (1949) have reviewed the use of licks especially in the Rocky Mountain National Parks of Canada and made studies to determine the role of the minerals obtained in such licks in the general health of wild animals. After several tests, these authors concluded as follows (p. 387):

> Our studies have not advanced the general knowledge of the function of natural licks in the physiology of wild ungulates much beyond that already obtained. The results are inconclusive and, taken in conjunction with similar studies of smaller scope made elsewhere in North America, lead to the conclusion (1) that sodium chloride is not necessarily the essential element; (2) that phosphorus is not the essential element in these licks; (3) that trace elements may well be the critical constituents in these natural licks; (4) that to arrive at conclusive results methods such as preference tests will probably be more productive then chemical analysis of the lick soils.

The use of licks by moose appears to reach its greatest intensity in spring. There was a definite decline in activity noted at licks in the St. Ignace Island area by late July, although animals continued to visit them until at least October. No sign of activity was noted in one of these well-used licks during a winter visit, although Hosley (1949) reports that Isle Royale moose used similar licks in winter. Cowan and Brink (1949) and other authors concur that little use of licks is made during the winter months. Observations in Ontario substantiate those of other workers that young of the year seldom if ever use such licks. Well-used licks are apparently less common in eastern North America than in the west, the best known being restricted to the islands of Lake Superior and a few scattered localities to the adjacent northwest.

No signs of salt licks could be found in Algonquin Provincial Park and efforts to feed salt by placing out salt blocks brought no response by moose, although they actually approached quite close to several stations. Rock salt was even placed adjacent to the natural licks on St. Ignace Island, but moose showed no interest in it and continued to drink from the muddy water. Perhaps the habit of licking commercial salt is acquired over a period of time, for Murie (1934) reports that moose commonly frequent "artificial licks" on Isle Royale. The term "salt lick" seems to be a misnomer. We found no indication of moose licking or eating the soil of such areas in Ontario and the actual salt content seems to vary considerably and frequently appears to be quite low. Murie (1934) had four samples of water and one of mud analysed from licks on Isle Royale. These proved to contain approximate proportions of salt in aqueous extract of from .10 to .25 per cent. The content of these samples was chiefly calcium sulphate and traces of sodium chloride. The mud sample contained much more of the latter than the liquid samples.

TABLE V.—Analysis of supernatant water from seven "salt licks" located in the St. Ignace Island area, Lake Superior, Ontario.

Sample	Hardness soap cons. power	Alkalinity	Solids			Parts per million						
			Total	Ignited	Loss on Ignition	Fe	Al	Ca	Na	Mg	SiO_2	Cl
Upper 1	258	292	506.8	310.4	196.4	2.4	5.8	88.8	62.0	2.46	4.4	64.0
Lower 1	174	126	498.0	290.4	207.6	.48	6.4	58.9	—	—	1.2	88.0
2	64	202	274.0	165.2	108.8	.40	2.7	9.4	56.5	.73	22.0	2.4
3	55	76	201.6	82.8	118.8	—	5.7	11.7	11.3	4.65	10.8	9.4
4	113	136	362.8	—	—	—	9.4	22.5	—	2.90	25.2	2.4
5	124	152	455.6	—	—	.02	3.8	42.5	—	7.20	27.6	45.0
6	102	172	355.6	—	—	.04	7.4	25.2	—	4.60	64.0	2.9

Chemical samples were taken from the mineral springs in the St. Ignace Island area and sent to the Ontario Department of Health who kindly provided a chemical analysis (table V). The great variation found in these samples, makes it difficult to arrive at any more conclusive findings than those outlined by Cowan and Brink.

Winter Browse Analysis

Size of sample

In the St. Ignace Island area a total of 1,000 plots, representing approximately 125 miles of browse survey lines, was analysed during 1947 and 1948. To test the adequacy of this sample, the total plots completed in 1947 and in 1948 are compared with the two year grand total in table II. The first group was selected to give the greatest geographic variation practicable as well as to provide as true a representative sample as possible. The sampling in 1948 was supplementary to that of 1947 in order to complete the greatest possible coverage of the islands. When comparing the results from the 318 plots of 1947 with the 682 plots completed in 1948, there seems to be little significant change in the over-all picture. Slightly heavier utilization was observed on mountain ash, red osier dogwood and willow, but in each instance there was also a slight increase in availability. Likewise in 1948 the slight decrease in the availability of balsam fir, highbush cranberry, red-berried elder and speckled alder was coupled with a slight reduction in utilization. When comparing the results from the 318 plots of 1947 to the combined total of 1,000, it will be noted that the forest composition, as expressed in availability, varied less than one per cent in all but four species (white cedar 1.8, white spruce 1.8, balsam 1.6, mountain maple 1.1). With one exception the estimates for individual species composition of the various foods eaten, as expressed by diet, was changed only two per cent or less. The twelve species providing the greatest amount of food for moose remained the same when the plots were increased from 318 to 1,000, although minor changes were made in the order of rank. Only one species, white pine, was added to the list of available species, but less than a dozen of these trees were seen anywhere on the islands during the two years. For most practical purposes there seems little doubt that 1,000 plots are adequate to provide a valid representative sample for the 140 square miles included in the study area.

Availability of winter moose foods

In order to evaluate certain factors brought out by browse analysis, a comparison of the results on the 1,000 plots with that of similar plots on Isle Royale analysed by Aldous and Krefting (1946) and Krefting (1951) is presented. Although 29 species are listed as available during winter in the St. Ignace area, only 22 were found to have been browsed to any appreciable extent, and 12 species provided 92.3 per cent of all food eaten. On Isle Royale, Aldous and Krefting (1946) found that 34 species were present in 1945 but that only 28 were browsed by moose while the top 12 species provided 92.5 per cent of the foods eaten, although their ratings included some species which do not occur in the St. Ignace area. Krefting (1951) found that the top 12 species provided 91.3 and 96.1 per cent of the diet in 1948 and 1950 with some slight changes in the species involved. When the utilization of the 13 species providing the greatest amounts of food from the St. Ignace area are compared with the Isle Royale results (fig. 2) some interesting conclusions are suggested. One of these is that the availability of a food species is more important in influencing the actual composition of the diet than palatability or individual preference.

In the St. Ignace Island area balsam fir constituted by far the greatest part of the total winter diet—27 per cent (see also *Stomach Analysis and Scatology*). However, it provided 30.9 per cent of all available food, more than three times the amount provided by any other species. On Isle Royale balsam fir rated third in the diet of moose in 1945 with 13.6 per cent (about one-half of that for St. Ignace) but provided only 9.8 per cent of available foods (about one-third of the amount available at St. Ignace). The 1948 browse analysis on Isle Royale indicates that balsam was rated first, constituting 13.5 per cent of the available browse and 21.8 per cent of the total food eaten. In 1950, however, balsam utilization dropped remarkably to only five per cent of the diet with little indication of reduction in relative availability. Krefting points out that in 1950 balsam fir was evidently affected not only by previous moose browsing but also by severe attacks of the spruce budworm. Some reduction in palatability with a shift of browsing pressure to other species may have influenced this reduced use of balsam fir on Isle Royale. Hosley (1949) reviews the data of Dyer (1948) on 12 "moose yards" in Maine to show balsam constituting 36.7 per cent of the available browse and 54 per cent of the total food eaten.

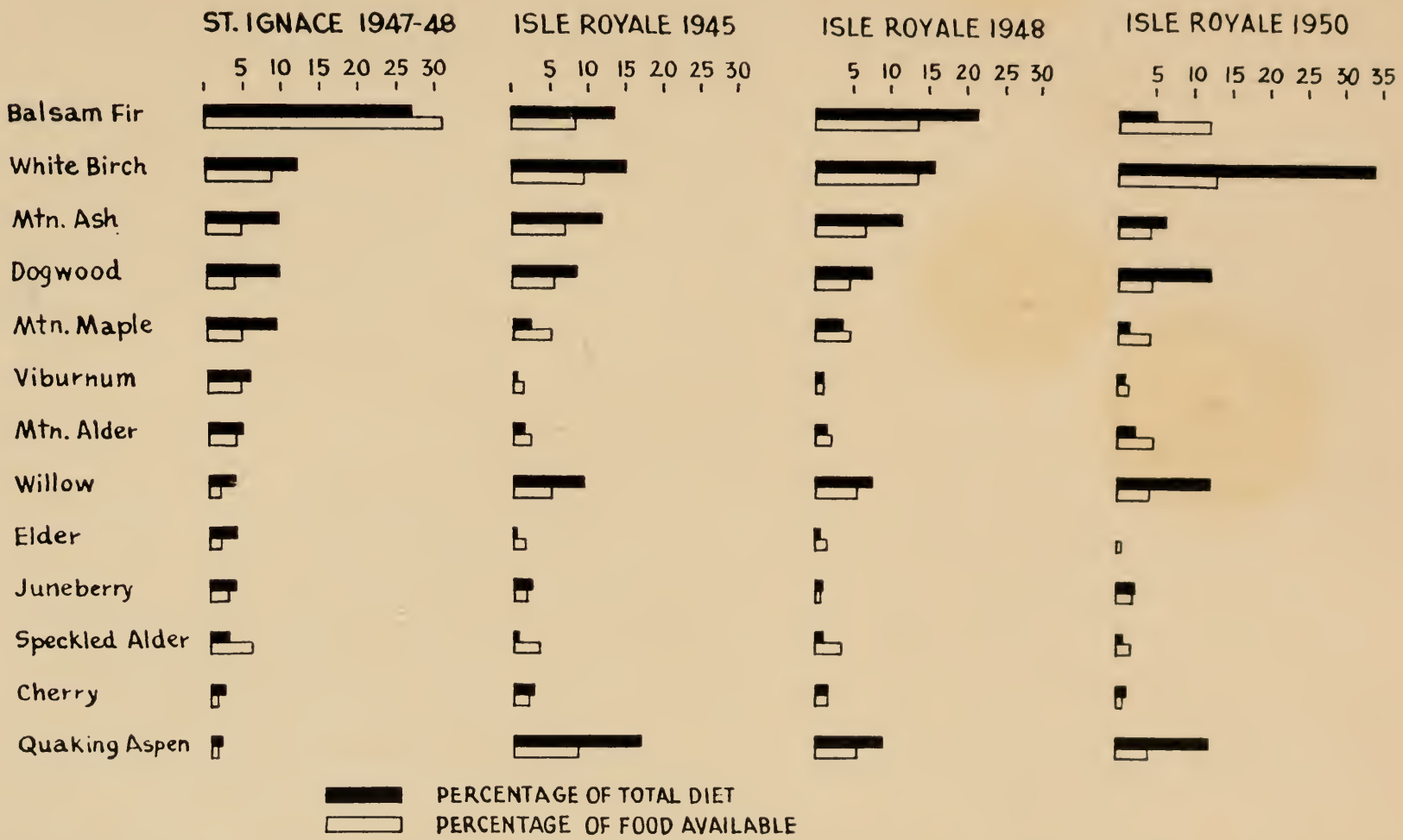

FIG. 2. A comparison of the utilization and availability of the principal moose food plants found on the St. Ignace Island area, Ontario with those of Isle Royale, Michigan.

Quaking aspen was listed as the number one winter food of moose on Isle Royale (16.9%) in 1945, but it provided only 8.7 per cent of the available food. In the 1948 survey it had dropped to fifth place in use percentage (5.4% of available browse and 9.0% of total food eaten). Hosley (1949) attributes this reduction to the lack of ability of this species to withstand heavy browsing. Krefting (1951) indicates that utilization of aspen in 1950 increased to second place (12.8% of diet) but its availability continued to decrease (to 4.7% of available food). Aspen rated only 13th in the St. Ignace area since it provided only 1.1 per cent of the available food (see *Habitat Studies*, and *Effect of Moose on the Habitat*).

Most other differences in food ratings between these two areas appear to be expressions of relative availability. The top nine or ten species in the diet in both cases seem to suggest such a correlation.

Effect of deer and caribou on St. Ignace browse analysis

It was impossible to segregate the effect of deer or caribou browsing from the final results in the St. Ignace area. Since the caribou population is extremely low, it is felt that its effect is probably insignificant. Undoubtedly there is more direct competition in the case of white-tailed deer. By comparing the total results with those on Isle Royale, where deer and caribou do not occur, some possible evaluation of their effect may be made.

Mountain maple, usually considered as an important deer food, rated fifth in the St. Ignace area with 9.1 per cent of the food eaten, but only 4.5 per cent of the available food. On Isle Royale it provided only 2.3 per cent of the diet and 5.0 per cent of available food in 1945, 3.3 per cent and 4.5 per cent respectively for 1949 and 1.7 per cent and 4.6 per cent for 1950. These differences bring up several complex factors in such comparisons. Deer undoubtedly account for a part of the increased browse on St. Ignace, but on the other hand two additional maple species are present on Isle Royale, which may be diverting some pressure from mountain maple. There, sugar maples provided 9.9 per cent of available food and 2.8 per cent of the diet in 1948. Red maple occurs on Isle Royale and accounted for 0.4 per cent of available food and 0.3 per cent of the diet for the same year. The maples of Isle Royale would together provide 6.5 per cent of the diet and 15 per cent of the available food for 1948. Studies in Algonquin Provincial Park

indicate the order of preference for maples by moose as follows: (1) striped or moose maple (*Acer pennsylvanicum*), (2) red maple (*Acer rubrum*), (3) mountain maple (*Acer spicatum*) and (4) sugar maple (*Acer saccharum*). The absence of other maples seems to have resulted in increased browse pressure on mountain maple, since the scarcity of deer, the height of browse and other factors suggest that moose must have accounted for over half of the browse of this species. If half of the browse were attributed to deer, mountain maple would rate seventh as a producer of moose food, which is still higher than any maple on Isle Royale. Dyer's 1948 data indicate that in Maine, mountain maple constituted 22.2 per cent of the available browse and 23 per cent of the food eaten which ranked it second in importance as winter moose food there.

Other species which show possible reflections of added browse by deer in the St. Ignace area include highbush cranberry, red-berried elder, raspberry and rose. Highbush cranberry rates sixth on St. Ignace with 4.4 per cent available and 5.2 per cent of the diet, while it rated only 16th on Isle Royale with only 1.4 per cent available and 0.7 per cent of the diet in 1945. It was listed as 1.2 and 1.2 in 1948, and 1.0 and 1.6 in 1950 (Krefting 1951). Similar disparities are noted for red-berried elder (26th for Isle Royale in 1945), rose (34th for Isle Royale in 1945) and raspberry which was not recorded as being browsed there. White cedar rated 17th as a producer of moose food on Isle Royale in 1945 (5.8% available and 0.7% of diet) and 21st on St. Ignace (3.0% available and 0.4% of diet) when using the browse survey method (see *Stomach Analysis and Scatology*). In 1948 the white cedar had increased to 1.6 per cent of the diet (dropped to 0.4 in 1950) providing only 4.5 per cent of the food available on Isle Royale (4.4 in 1950). The low utilization of this important deer winter food on St. Ignace seems to indicate that the past low deer populations have had relatively little serious effect on the results of the moose browse analysis.

Palatability preference

Several of the less abundant species seem to be preferred foods of moose, but their low availability prevents them from actually becoming more important items in the diet. The degree of browsing of available foods (fig. 3) gives a partial indication of palatability preference of moose for various species, but in several instances these expressions of palatability are more or less invalidated. Such species as white birch, mountain ash

and quaking aspen occur in a high percent of the plots as extremely small seedlings which would be covered by snow during winter or as mature trees providing no browse within reach of moose. Aspen shrubs and saplings are rare. This has certainly prevented a true representation of moose preference for quaking aspen.

To obtain further indications of preference, equal-sized branches of quaking aspen, balsam poplar, white birch and speckled alder were cut in the summer of 1947 and left overnight

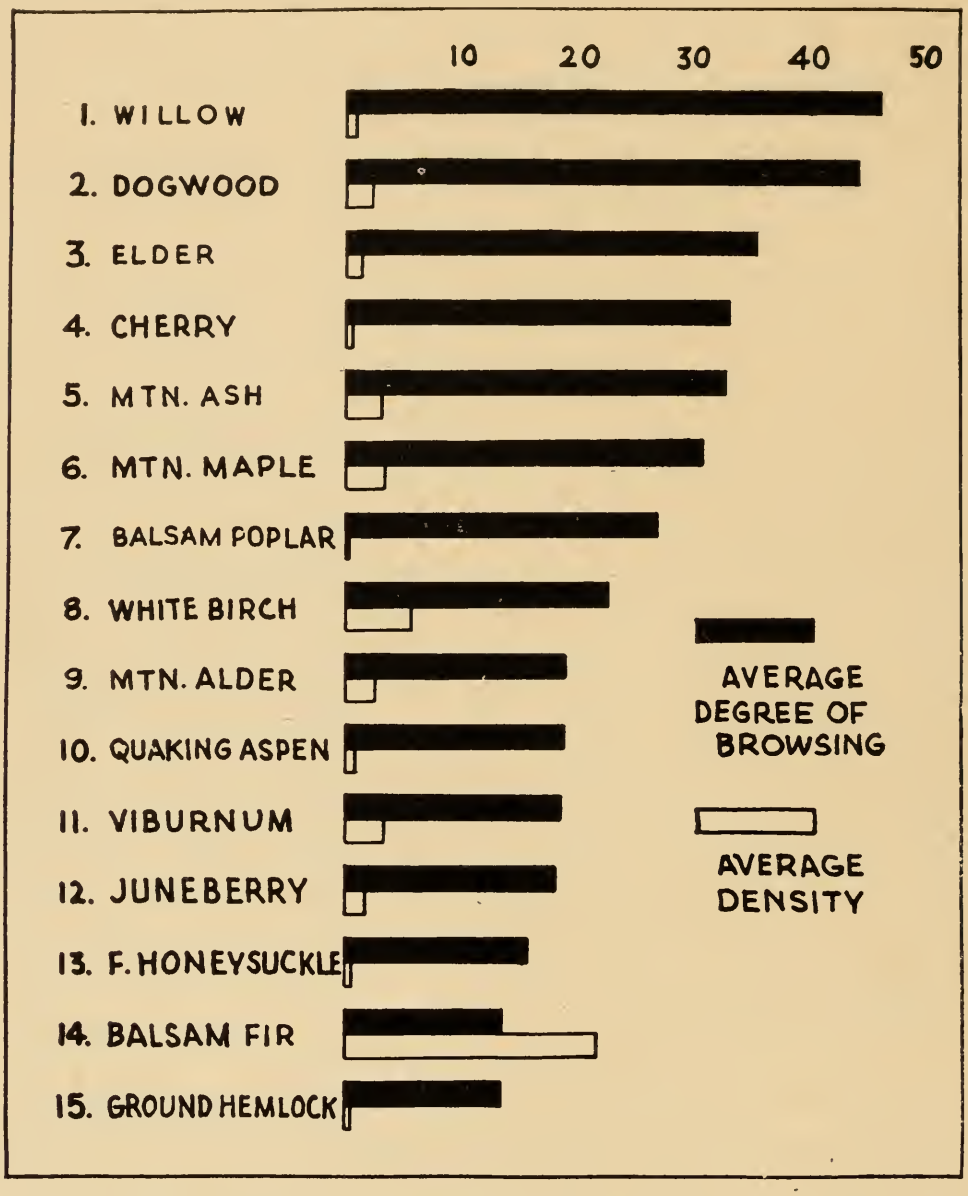

FIG. 3. Palatability preference for certain moose foods as indicated by the average degree of browsing found on 1000 plots in the St. Ignace Island area.

by a well-used salt lick. The next morning we found that moose had completely stripped the aspen of every leaf and had chewed off most of the smaller twigs and branches. Balsam poplar and white birch were browsed only moderately and the speckled alder was untouched.

In early spring of 1946 a similar experiment was conducted except that mountain ash was also added to choices. We were unable to return immediately to check the results, but after an interval of about one week similar results were noted. The mountain ash was heavily utilized, ranking about second to quaking aspen.

It seems evident that the actual amount of each food species which moose will consume is correlated and interrelated not only with the palatability and availability of that species, but also with the presence, availability or absence, in any given area, of all other food plants of various palatability levels.

Other winter food species

In areas east of the northern Great Lakes region several additional species are utilized by moose. Beaked hazelnut (*Corylus rostrata*) is frequently more abundant and more heavily utilized in more eastern regions. Gray birch (*Betula populifolia*) is listed as one of the "chief" foods of moose in Maine by Lamson (Walcott, 1939). Dwarf birch (*Betula glandulosa*) is probably a preferred food where available. Hobblebush (*Viburnum alnifolium*) is utilized in Algonquin Park, Ontario. Cameron (1948) lists withe-rod (*Viburnum cassinoides*) as an important food in Nova Scotia and nanny berry (*Viburnum lentago*) is listed as a chief food of moose in Maine by Lamson (Walcott, 1939).

Oaks and basswood (*Tilia americana*) are utilized by moose, the latter being regarded as one of the "principal" winter foods in Minnesota (Manweiler, 1941); however, their status as moose food needs clarification.

Moose undoubtedly sample a great many other species which they never eat in quantity. The following appear to be in this class: red pine (*Pinus resinosa*), tamarack (*Larix laricina*), large toothed aspen (*Populus grandidentata*), ironwood (*Ostrya virginiana*), beech (*Fagus grandifolia*) and white ash (*Fraxinus americana*).

Moose occasionally feed on *Usnea*. The extent and importance of this source of food is not known.

Moose Stomach Analysis and Scatology

Stomach analysis

Laboratory examinations of one-quart samples from 24 stomachs of Ontario moose and one each from Manitoba and Quebec, were made in order to further check and verify data on food habits obtained by other methods. Mr. V. H. H. Williamson, working in the Wildlife Food Habits Research Laboratory of the Royal Ontario Museum of Zoology under a grant from the Research Council of Ontario, has carried out the detailed examinations of both moose stomach contents and winter droppings (table III).

In the stomachs of moose taken from October 19 to May 5, balsam fir was found in all but three cases, one being from an area in Manitoba where this species does not occur. White cedar occurred in small amounts in four and as a large portion of one stomach, the latter from a diseased animal. This species occurred in roughly 19 per cent of late fall and winter specimens. Of the total for all months, willow occurred more frequently than any other deciduous species (16 or 66.2%). White birch was found in 11 (42.4%), beaked hazel in 10 (38.6%), quaking aspen in 9 (33.6%), cherry in four cases, dwarf birch and dogwood in two each and juneberry and maple in only one each.

Hosley (1949) lists the results of examination of one moose stomach from Maine, taken in April, as follows: Balsam fir, 45 per cent; birch (sp.?), 45 per cent; maple (sp.?), 1 per cent; northern white cedar, 1 per cent; sheep laurel (*Kalmia angustifolia*), trace; and willow, trace.

Scatology

From late fall to early spring the droppings of moose are composed of persistent spherical or oblong pellets. Skuncke (1949) points out that the shapes of these pellets are different for the sexes in Sweden, that of the bull being more spherical while that of the cow is more elongate or ovoid. A definite dimorphism has been noted in the droppings of North American moose but apparently the constancy of these sexual differences has not been studied or confirmed here. With the change from winter to summer diet, the droppings likewise show a transition toward the typical summer droppings which become amorphous or viscous from the herbaceous diet. Since the needles of conifer species eaten during winter pass through in an identifiable

state, it seemed desirable to obtain still another check on the surprisingly high utilization of balsam. A sample of five pellets was collected at random from various deposits from both the Algonquin and the St. Ignace study areas, and brought into the laboratory. The results of their examination by Mr. Williamson are given in table IV.

On careful examination of 1,055 individual pellets balsam fir was found in each. In Algonquin Provincial Park, where balsam is much less abundant, white cedar and hemlock are eaten in much larger proportions. Hemlock is apparently an important balsam supplement in the Canadian biotic province. White cedar is sampled freely but is rarely eaten in abundance. Murie (1934) found that moose had eaten the bark from this species during high population levels on Isle Royale. Hosley (1949) points out, from the first two browse analysis surveys on Isle Royale, that the utilization of white cedar had more than doubled between 1945 and 1948. This was regarded as an indication of heavy over-browsing.

Ground hemlock (*Taxus canadensis*) is apparently too scarce in either locality to constitute an important item in the diet of moose. Murie (1934) reports this species as being a highly palatable moose food during both summer and winter. Murie, as well as Aldous and Krefting (1946) regards this species as an important index to general browse conditions. It is still abundant on small islands off Isle Royale and on the Slate Islands in Lake Superior where moose do not occur.

Discussion

In a general consideration of the basic importance of food in the ecology of an animal such as moose, special attention should be devoted to the effects of an inadequate diet on populations of the species. This seems especially important in view of the fact that the effects of malnutrition are frequently obscured by some secondary manifestation.

Assuming that a population of moose is found in an area of inadequate food supply, one might logically contend that the animals would be faced with a choice of either migration or starvation. Little is known of the normal reactions of moose under such circumstances, but it is known that deer will persist in an area when faced with starvation, even though adequate food supplies may be available a relatively short distance away.

The question then arises as to what happens to the population that cannot or does not migrate. If no other factor interferes, death from actual starvation would ultimately result. This manifestation of malnutrition is perhaps the most drastic and most easily recognized. In actual cases, however, the population is usually greatly reduced before such a point is reached. Such factors as diseases, parasites and predators frequently combine with malnutrition to lower the number of animals before actual death from starvation is reached. This well-known population phenomenon has been discussed for a great many animals, but one gains the impression that the basic importance of food or lack of food is often not properly appreciated. Over much of Ontario there has existed a low and rather static moose population. Although perhaps not faced with starvation, the moose in many areas find a rather marginal food supply, especially in late winter.

The failure of moose to show appreciable increases over a period of years in such areas cannot always be logically explained on the basis of constant suppression by such factors as diseases, parasites or predators, even though no visible signs of starvation may be apparent. If these were limiting factors, one would expect to find a certain amount of marked fluctuation in the population as well as a regular and direct manifestation of one or more of these factors. Furthermore, in adjacent areas where diseases, parasites and predators should have a similar effect, high populations are often maintained.

The failure of low populations to increase appears to be more directly correlated with a low rate of reproduction. The fact that moose do not increase in such areas while high populations are being maintained in others suggests that the local habitat itself must be influencing this differential rate of reproduction or survival. The most logical correlation within the habitat is with food supply. Perhaps quality, rather than quantity, of available food is of prime importance in this connection. Morton and Cheatum (1946) have demonstrated a correlation between nutrition and the rate of births in New York deer and have found that in areas of depleted food supply the rate of ovulation is significantly lower than in the more favourable areas. If true for deer, this correlation probably exists with moose as well.

After fertilization the growth and development of the embryo to a healthy birth is dependent on the cow obtaining adequate

quantity and quality of nutrition. Even then, food is of basic importance to the cow as well as the calf in connection with the ability of the cow to produce sufficient milk to successfully raise the calf, and at the same time have adequate vitality to protect the young from predators.

Although adequate nutritional studies of various moose foods have not yet been carried out, the general food habits of moose indicate that a variety of foods is an essential factor in a balanced diet. A great quantity of poor foods or of only two or three species apparently will not maintain a healthy moose population. While it is well known that the availability of food is a limiting factor affecting the immediate carrying capacity of any given habitat, the role of the habitat (through food supply) in predetermining the potential population level needs further emphasis and investigation.

Habitat Studies

As a herbivore, the moose is directly affected by the floral composition of its habitat. Many factors combine to influence the plant life and thereby become important in the ecology of moose. Climate, soils and time combine to shape the basic factors in the environment. However, several additional factors become interrelated to create considerable variation in local habitats. Chief among these are the various plant associations and their ecological succession, together with the factors which influence them, such as fire, commercial operations of civilization, and the activities of the associated animal communities.

Plant Associations and Ecological Succession

Favourable habitat of moose is basically dependent on continual forest succession or regeneration. Moose populations apparently reach their maximum in the early stages of succession and decrease as the forest reaches maturity. Many important foods of moose are found only in areas where the mature or climax forest has been removed, thus allowing such food species to appear. In dense mature forests, shading by the upper canopy creates natural pruning of lower branches and prevents growth or regeneration of most seedlings and shrubs. Mixed, rather than pure, stands of forest species tend to be required for favourable moose habitat. Although the general environmental conditions found in the St. Ignace area of Ontario are

acceptable to moose, there are certain local areas which definitely seem more favourable than others (fig. 4). An excellent example of a good fall and winter area for moose is found in Otter Creek Valley on St. Ignace Island.

Otter Creek Valley, St. Ignace Island

This valley comprises roughly two square miles with three small streams traversing parts of it. In addition to the heavily browsed conditions, there is further evidence of the attractiveness of this area during winter months. The number of winter droppings found on the browse analysis plots was 151 per acre compared to 37 per acre for the entire study area including Otter Creek Valley. A total of 47 single shed antlers was found within this two square mile area compared to 53 for all the rest of the study area. The ratio of freshly dropped to older shed antlers was roughly the same for both Otter Creek Valley and the total area. On September 16, 1947, no fewer than 40 "beds"

FIG. 4. An example of moose habitat on Simpson Island, Ontario, 1947.

where moose had lain down were found during a two hour hike on the east side of this valley. All of these "beds" appeared to have been made within the previous week. A total of 26 such spots was found on a similar hike through the central and western sections of the valley September 22.

Parts of Otter Creek Valley were either logged or burned several years previously. A comparison of the winter browse analysis for Otter Creek Valley with the total of the study area brings out certain features of favourable winter habitat (table VI). One of the important factors, suggested by this comparison,

TABLE VI.—Winter browse analysis of Otter Creek Valley and areas burned in 1936, compared with the total St. Ignace area.

Species	Otter Creek Valley (55 plots)		Areas burned in 1936 (55 plots)		Total St. Ignace (1,000 plots)	
	% food eaten	% food available	% food eaten	% food available	% food eaten	% food available
1. Balsam fir	16.4	18.3	1.9	11.0	27.0	30.9
2. White birch	6.4	4.5	65.6	47.9	12.0	8.2
3. Mountain ash	4.5	2.7	3.8	1.7	9.4	4.4
4. Red-osier dogwood	16.7	9.6	—	—	9.4	3.3
5. Mountain maple	25.4	14.1	1.3	.5	9.1	4.5
6. Highbush cranberry	6.5	6.6	.1	1.0	5.2	4.4
7. Mountain alder	7.5	10.0	1.0	.7	4.5	3.7
8. Willows	4.0	2.4	11.9	7.3	4.2	1.4
9. Red-berried elder	2.5	1.8	4.2	2.4	3.9	1.7
10. Juneberry	2.7	2.2	.2	.5	3.1	2.6
11. Speckled alder	.5	7.8	.2	.1	2.7	5.6
12. Cherries	4.1	2.3	2.9	3.3	1.8	.8
13. Quaking aspen	.3	.3	6.5	5.3	1.4	1.1
14. Raspberries	tr	2.3	.2	4.4	1.2	4.6
15. Fly honeysuckle	1.2	.9	—	—	.8	.8
16. Balsam poplar	.3	.2	—	—	.7	.3
17. Beaked hazelnut	—	—	—	—	.7	.2
18. Roses	.2	2.2	.1	1.1	.7	1.7
19. Ground hemlock	—	—	—	—	.6	.7
20. Salmon berry	.3	.9	—	—	.5	.6
21. White cedar	—	.1	tr	.1	.4	3.0
22. Currants and gooseberry	tr	.7	.1	2.9	.4	1.9
23. White spruce	—	4.0	—	7.6	tr	6.9
24. Black spruce	—	6.0	—	1.8	tr	6.6
25. Nine-bark	—	—	—	—	tr	tr
26. Tamarack	—	—	—	.1	—	tr
27. Junipers	—	—	—	—	—	tr
28. Jack pine	—	—	—	—	—	tr
29. White pine	—	—	—	—	—	tr

is the more nearly equal availability of several preferred food species. In Otter Creek Valley balsam fir does not constitute such a high proportion of the available food and consequently

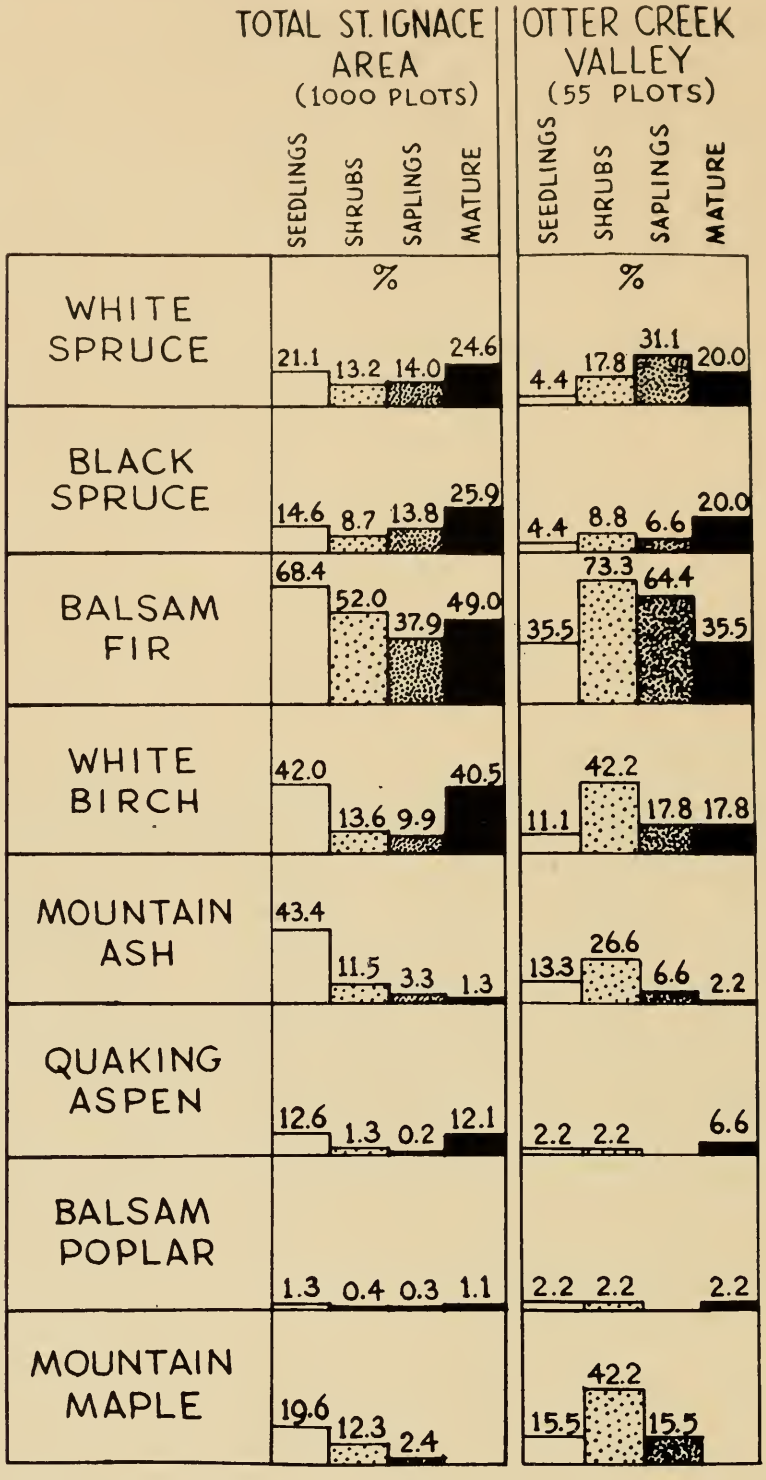

FIG. 5. The age composition of the principal forest trees in the St. Ignace Island area, based on percentage occurrence of each age classification on the total plots examined.

provides a smaller per cent of the diet. This seems further to indicate that the great importance of balsam fir in the diet is more closely related to availability than to palatability.

These data tend to substantiate other general observations which indicate that moose prefer areas producing the greatest variety of available food. Large tracts of land providing only two or three species of food, even in abundant supply, are rarely heavily utilized by moose in Ontario. Local "pure stands" are frequently utilized when other types of food are available nearby. Even within local favourable habitats, the highest degree of browsing seems to be associated with small openings or clearings.

Other characteristics of Otter Creek Valley which reflect favourable conditions for moose are found in a study of the age composition of the principal forest trees (fig. 5). Chief among these are the higher proportions of shrubs and saplings.

Age composition of the principal forest trees of the St. Ignace area

While carrying out the winter browse analysis survey, the forest trees on each plot were classified and recorded by age groups. The over-all age composition for the study area is compared with Otter Creek Valley in fig. 5. The age pattern for several of the preferred moose food species in Otter Creek Valley seems to approach an ideal winter moose habitat.

In considering the general age composition for the islands as a whole, the spruces may be used as indications of the age development of the forests since they are practically never browsed and thus not affected by moose or deer. Constant heavy browsing by moose has undoubtedly altered the age composition in certain other species.

For the entire St. Ignace area, seedlings of all species occurred on a higher percentage of the plots than did shrubs. In Otter Creek Valley the reverse was true with shrubs generally being more abundant than other age classifications, with the exception of spruces and poplars.

There can be little doubt that the age and the species composition, as represented in Otter Creek Valley, are among the prime factors contributing toward optimum winter habitat.

Plant succession in Algonquin Provincial Park

This area is fairly characteristic of the Canadian biotic province in which sugar maple and yellow birch form the climax

forest. Moose are largely dependent on the successional stages for suitable habitat within this region. Thus shore line associations and burned areas form important elements in moose habitat of the Canadian biotic province.

As outlined by Dice (1938; 1943) and others, the chief species that succeed burning are the aspens and white birch. In certain old burned areas a considerable amount of red maple was found associated with these species. Close examination of a small island at the west end of Longbow Lake that had been burned over a year previously revealed that all the chief tree species had been killed out with the exception of red maple. In a few cases these trees were still alive while the spruces, white pine, hemlock, balsam, white birch, yellow birch and sugar maple were all dead. Many of the red maple trees were sprouting from the base of the trunk although the tops were apparently dead. It appears that the resistance to less intense fires by red maple allows this species to maintain itself in certain successional stages of development following fires.

A winter "yard", Algonquin Provincial Park

A local and well defined winter "yard" in Algonquin Provincial Park afforded opportunity to check existing conditions in an effort to appraise a few of the factors which attracted or maintained a winter concentration of moose. The area comprised about four or five acres along the northeast shore of McIntosh Lake. About three acres of the area was surveyed and staked into quadrats. The species composition and relative availability of the trees and shrubs in the "yard" based on 102 plots (16½ feet by 16½ feet) are given in table VII. A total of 391 piles of moose droppings was counted on 14,400 square yards of the area. In addition, the dropping counts also showed deer, 136; grouse, 16; and rabbit, 1.

The "yard" was situated on the base of a southern slope of a hill forming a long narrow band between a pure climax association of sugar maple and yellow birch on the upper slope and the rocky shoreline of the lake which was fringed by white cedar. The evidence of winter browsing and winter droppings were almost wholly confined to this narrow strip. Their termination at the edge of the hardwood climax was quite striking. The presence of both deer and moose in the area made it impossible to segregate the browse effect of these two mammals. Balsam fir was by far the most abundant and most heavily browsed of all species present. The habit of riding down or breaking out the

tops of shrubs and saplings might give some index to moose activity in the area. A total of 164 (24.5%) of the balsam shrubs and saplings had the tops broken out (shrubs 137 or 31% and saplings 27 or 11.5%) on 0.64 of an acre. In addition, the following shrubs and saplings were found with tops broken by animal activity; mountain maple, 41; sugar maple, 8; hobblebush, 3; beech, 2; striped maple, 1; and black spruce, 1.

Since the limits of this area of moose winter concentrations appeared to be closely correlated with the local distribution of balsam fir, there seems little doubt that the heavy utilization of the species gives corroboration of its basic importance in the ecology of moose in the eastern part of its range.

TABLE VII.—Plant composition of an Algonquin Provincial Park winter moose "yard" (102 plots in a 3 acre area).

Species	% of plots present	% of browse available
White pine	31	1.2
White spruce	8	.7
Black spruce	70	18.7
Hemlock	74	5.7
Balsam fir	100	42.2
White cedar	46	2.8
Beaked hazelnut	17	3.4
White birch	14	1.2
Yellow birch	56	4.8
Speckled alder	8	2.6
Cherries	4	.3
Juneberry	31	1.8
Beech	5	.2
Mountain ash	23	2.5
Striped maple	9	.9
Mountain maple	35	6.5
Sugar maple	15	2.1
Red maple	21	1.1
Hobblebush	14	1.3

The effect of forest succession upon the nutritive values of moose food plants

In central British Columbia, Cowan, Hoar and Hatter (1950) carried out studies of three stages in forest succession growing under virtually identical conditions of soil and climate to determine the quantity of available palatable browse; carotene and ascorbic acid content of available palatable and unpalatable trees and shrubs; and to carry out analysis of values for moisture, protein, carbohydrate, ether extractives and total mineral

content. Most of their analyses were confined to the winter dormant period. The earliest stage (Area 1) was six years old, while the second was an intermediate stage, and the third a mature forest.

In summarizing the results of these studies in British Columbia, the authors conclude as follows:

> It is determined that the forest changes studied involved a reduction in quantity of palatable browse to about one-third; that there is an increase of carotene values and possibly of total mineral content in the vegetation on more advanced forest areas, but that in ascorbic acid content, ether extractives, total carbohydrates, and proteins, the vegetation upon the younger forest areas is superior to that on the older areas.
>
> It is concluded, therefore, that the declining carrying capacity noted in a forest approaching its climax stage results from decreases in both the quantity and quality of food produced.
>
> It is further concluded that the most desirable winter range for moose is one upon which there is a variety of palatable species, predominantly in an early stage of growth, but with an intermixture of older forest stands bearing palatable coniferous trees (Cowan, Hoar and Hatter, 1950, p. 249).

The latter conclusion agrees almost identically with that reached by other methods in Ontario studies (Peterson, 1949).

Effects of Fire

Forest fires have undoubtedly been a most important agent affecting forest succession. The wasteful destruction of valuable timber and wildlife and the resultant erosion and flooding is often offset, in part, by the creation of more favourable habitat for moose and other wildlife.

The moose of Isle Royale had so completely depleted their food supply by 1935 that ultimate starvation seemed inevitable.

> In 1936 fires burned over approximately one-fourth of the island. These eliminated a large part of the browse supply for 2 or 3 years, but in the long run have been one of the greatest factors in permitting a comeback of the moose. Today the 1936 burned area supplies more browse than the remainder of the island combined (Aldous and Krefting, 1946, p. 296).

In 1936 a small area was burned on the southwest portions of both St. Ignace and Simpson Islands, Ontario. A total of 55 browse plots was analysed in these two areas. The results are summarized in table VI. White birch is the outstanding species from the standpoint of both the amount available and amount eaten. Following in the order of amounts available were balsam fir, white spruce, willow, quaking aspen, red-berried elder, mountain ash and cherry. These two small burned areas were providing a significant proportion of the entire islands' available white birch, willow and quaking aspen.

Utilization of these two burned areas seems to reach maxima in late fall and early spring. Since balsam fir is eaten only during the winter months, this undoubtedly affects the low amount indicated in the winter diet for these areas. There is little protective cover in these areas but they are sufficiently small that moose effectively utilized them by ranging out from nearby cover.

There are in Ontario some extensive burned areas into which moose rarely venture. Preliminary investigations suggest that large burned-over tracts do not normally become heavily populated by moose until a balanced winter and summer habitat becomes available. Key factors under such circumstances seem to be (1) sufficient variety of foods for all seasons including, (2) aquatic vegetation in summer and (3) balsam fir in winter.

Effects of Lumbering Operations

The over-all effects of various types of lumbering operations cannot be properly evaluated on the basis of past studies and should be the subject of further research. A few generalizations may be discussed, however, in order to present certain aspects of the problem that have been suggested.

The process of forest succession which follows the destruction of forest resources by fires can be, to a certain degree, initiated by certain types of lumbering operations. As suggested by the results of large fires, clean cutting of vast areas appears to reduce maximum utilization by moose for a longer period than other methods of cutting, although this length of time is undoubtedly shorter than that following fire. Selective cutting, on the other hand, frequently fails to reduce the forest canopy sufficiently to allow successional growth. Areas observed in Ontario on which selective cutting had been followed usually provided little growth of important food plants and under several situations were grown up with dense stands of raspberries.

In the St. Ignace area of Ontario it seems possible that selective cutting of quaking aspen for paper pulp logs may have been one of the factors affecting the present low supply of this species. However, selective cutting of quaking aspen is probably less important than the effect of moose and other animals together with the general ecological development of the area.

It seems reasonable to assume that the physical operations of lumbering have little serious detrimental effect on moose unless wilful disturbance or shooting of the animals is carried out.

In fact, moose are frequently reported to take advantage of the increased availability of the tops of the freshly cut trees.

In summary, preliminary studies suggest that under most circumstances the clean cutting of smaller spots or strips will normally increase the available food supply and thereby improve the habitat for moose. The relationships of moose and various other types of lumbering operations depend on many local conditions and therefore cannot be included in the scope of the present work. Apparently no special study of this subject has been undertaken in North America, although some progress in this direction has been made in Sweden. It seems reasonable to assume that the foresting practices carried on in that country have had a beneficial effect on the moose habitat. The moose has increased to such a point in Sweden, in spite of high annual kills, that the Government recently established a Royal Commission to enquire into what steps should appropriately be taken to prevent and minimize damages caused to the forests by moose (Hamilton, 1947). Certainly the lumbering operations in that country have had little or no detrimental effect on the moose habitat or moose numbers.

Effects of Forest Insects

The habitat of moose is sometimes seriously affected by "outbreak" infestations of forest insects which destroy certain food species. In areas of heavy outbreak the spruce budworm (*Chloristoneura fumiferana*) has caused remarkably high mortality in balsam fir. The over-all effect of spruce budworm in Ontario has been reviewed in a brief presented before the Ontario Royal Commission on Forestry in 1946 by the members of the Forest Insect Investigations Unit (Canada, 1946).

In many areas spruce budworm has caused over 50 per cent mortality in balsam fir with several instances of 100 per cent. Such drastic reduction in this important winter food undoubtedly has a serious effect on local moose populations.

As in the case of the destruction of habitat by fire, some compensating factors seem to follow spruce budworm destruction of balsam fir. According to Dr. M. L. Prebble, officer-in-charge of the Forest Insect Laboratory at Sault Ste. Marie, Ontario, and others (personal communication) such areas frequently show rapid regeneration of young balsam fir. In fact, Dr. Prebble has summarized preliminary findings by the following statement (personal letter):

Spruce does not seem to do well when the stand is opened up by budworm killing, despite somewhat heavier killing of balsam fir than spruce. This is an unusual situation which has not always been appreciated by investigators who have sometimes spoken of the spruce budworm as a corrective influence in establishing proper relationship between balsam fir and spruce. Actually, killing of the mature balsam by the spruce budworm seems to have the effect of increasing the balsam content of the succeeding forest.

The speed of balsam regeneration seems to depend on local ecological conditions. As pointed out by Dr. Prebble, frequently areas of dead balsam fir will be taken over by dense growth of raspberries and other quick growing species which in turn make the establishment and survival of conifer seedlings very difficult. For example, he writes of such an instance as follows: "In one such area that was examined last year [1947] balsam fir seedlings, about seven years old and only about six inches high, were found in fair number under the heavy overgrowth of raspberry, et cetera."

In other areas regeneration is extremely rapid. On this point, Dr. Prebble makes the following comment: "At the present time, it appears that much of this advance growth was already established before killing of mature timber and shoots ahead rapidly when the stand is opened by killing."

There can be little doubt that this destruction of balsam fir has been at least a temporary factor limiting the winter food supply of moose in Ontario. It seems quite possible that where deer and moose are competing for winter food in the same general area, the reduction of this important moose food creates a habitat change which favours the deer.

In New Brunswick it is reported that the spruce budworm killed off large stands of balsam between 1915 and 1920 (New Brunswick, 1944). As indicated by hunter kill figures, the trend in moose and deer populations in that Province appears similar to those in Nova Scotia where moose generally decreased after 1931 and deer began increasing at a remarkable rate (Nova Scotia, 1948). The relative importance of the influence of spruce budworm on the relationship between moose and deer is not known.

In summary, it appears that forest insects, especially the spruce budworm, constitute important factors in the general ecology of moose. The complex role of forest insects in various biotic communities, in terms of their effect on such forms as moose and deer, is as yet poorly understood. Further studies along these lines are needed.

The Effects of Moose on the Habitat

Large herbivores, perhaps as much as any other group, frequently exert a great and noticeable influence on the ecological composition of local habitats or communities. In Sweden the high moose or "elk" population has caused so much damage to forests, especially to reforestation projects, that measures beyond normal hunting pressure, have been investigated in order to reduce damage by further reduction of moose numbers (Hamilton, 1947).

Moose in Ontario have never created a similar problem but they apparently have been responsible for definitely altering the forest composition in some areas. The over-all and detailed effects of moose on the general environment cannot be determined in such a short study. A long-time study based on an adequate series of permanently fenced plot enclosures should afford data on a great many fundamental factors which directly or indirectly affect both the moose and the habitat. A few of these factors seem apparent on the basis of past studies.

On Isle Royale, and perhaps St. Ignace, moose have apparently been responsible for a great decimation and suppression of ground hemlock. The same applies to the aquatic plants, especially the water lily group. Several species of trees are being browsed to such an extent that normal regeneration is being inhibited or stopped almost completely. This seems especially true of quaking aspen in the St. Ignace area. Moose appear to be one of the chief factors responsible for the unusually low occurrence of shrub and sapling stages (fig. 5).

In the case of such species as mountain ash, which rarely attains the size of mature trees, it is more difficult to assess the effect of constant pruning by moose. The amount of heavy utilization observed on this species certainly must influence the number that mature beyond the shrub stage.

The resultant species composition of an area is undoubtedly greatly affected by the differential ability of various species to withstand constant heavy browsing by moose or other mammalian species. Continued close pruning of one species may frequently allow a related, less palatable species to become dominant. This seems particularly true in certain cases with balsam fir and spruces (fig. 6). Constant pruning of the annual growth and even partial destruction of balsam has allowed the unbrowsed spruces to speed up a domination of many local areas.

Moose preference for semi-open or small clearing areas has frequently been effective in maintaining such communities by

constant browsing (fig. 7). In other areas certain species are so completely destroyed by such heavy use that an entirely new plant association may result.

Such changes may take the form of successional replacement by more hardy or by less palatable forest species. In certain cases moose appear to be a contributing factor in the establishment and maintenance of grassy swales and clearings within a boreal forest community.

Preliminary investigations seem to suggest that in areas where an apparent balance of the moose population with the carrying capacity of the habitat exists, moose tend to help maintain or improve their own habitat conditions. In areas of extremely low populations the habitat usually matures or passes through normal successional stages to become less favourable for moose, while in over-populated areas moose may tend to suppress regeneration of important moose foods which in turn may also result in less favourable forest composition.

FIG. 6. Balsam fir showing the effect of constant pruning by moose. Pruning has resulted in a temporary increase in actual volume of available browse in this region, although unbrowsed spruces are also increasing.

FIG. 7. Suppression of regeneration of forest species by moose. Small clearings are apparently maintained by heavy moose browsing.

SUMMARY

A system of winter browse analysis developed by Aldous (1944) has been employed in the St. Ignace area of Ontario. The method is described and various aspects of its use are discussed. A total of 1,000 sample browse plots of 1/100 acre were analysed in 1947 and 1948. In 1947, 318 plots were completed and in 1948 an additional 682 were analysed. The increase from 318 to 1,000 plots created only minor changes in the final results, indicating that the number used was adequate to provide a valid representative sample for the 140 square miles included in the study area.

Using this system of winter browse analysis the following data has been computed for each species of plant available during the winter months in the St. Ignace area:
(1) the percent of plots in which it was present, (2) its average density, (3) the average degree that it has been browsed, (4) its percent of total food eaten, and (5) its percent of the total food available.

A total of 29 species was found to be available during the winter in the St. Ignace area although only 22 were found to

have been browsed to any extent. Of the more important food plants, 12 species provided 92.3 per cent of all food eaten.

By comparing the results of winter browse analysis in the St. Ignace area with that of Isle Royale by Aldous and Krefting (1946) and Krefting (1951), a study of certain factors has been possible. The availability of food species seems more important in influencing the actual composition of the diet than palatability or individual preference.

Assessment of the relative importance of the effect of caribou and deer suggests that the former was insignificant and the latter was of minor over-all importance, although certain species of plants appear to have been significantly affected.

A study of the importance of palatability or individual preference for certain species indicates that the actual amount of each species moose will consume is correlated and interrelated, not only with the palatability and availability of that species, but also with the presence, availability or absence, in any given area, of all other food plants of various palatability levels.

Further study of winter food habits, as well as general food habits throughout all seasons, was made by (1) direct field observations during all seasons, (2) analysis of samples from stomach contents of 26 moose taken throughout the year, (3) analysing the conifer contents of 1,055 pellets from 211 moose dropping samples, and (4) by feeding experiments in the vicinity of well-used "salt licks".

Considerable seasonal variation was found both in the types of foods eaten and in methods of feeding. Various aspects of these variations are discussed.

The 12 most important species in the St. Ignace area from the standpoint of per cent of food eaten during winter were found to be ranked in the following order: (1) balsam fir, (2) white birch, (3) mountain ash, (4) red-osier dogwood, (5) mountain maple, (6) highbush cranberry, (7) mountain alder, (8) willows, (9) red-berried elder (?), (10) juneberry, (11) speckled alder, and (12) cherries.

As indicated by the average degree of browsing, the 12 most highly preferred winter foods were found to be ranked as follows: (1) willow, (2) red-osier dogwood, (3) red-berried elder (?), (4) cherries, (5) mountain ash, (6) mountain maple, (7) balsam poplar, (8) white birch, (9) mountain alder, (10) quaking aspen, (11) highbush cranberry, and (12) juneberry. Other studies would indicate that quaking aspen usually ranks

higher on the preferred list, and that beaked hazelnut and dwarf birch are also included as preferred species when available.

Balsam fir was found to be the most abundant and apparently the most important winter food of moose in Ontario. However, it was practically untouched during the summer months. In the St. Ignace area it occurred on 93 per cent of 1,000 plots and provided 30.9 per cent of the available winter food and 27 per cent of the total winter diet. It was found in varying degree up to 100 per cent in a great majority of non-summer moose stomach content samples examined and occurred in 100 per cent of 1,055 pellets from 211 dropping samples.

Favourable habitat of moose is basically dependent on continual forest succession or regeneration. As a forest reaches maturity or its climax it becomes less favourable for moose. There is a decline in both quantity and quality of moose food nutrients as ecological succession proceeds towards a climax. Mixed, rather than pure, stands of forests appear to be essential to maximum utilization by moose. Otter Creek Valley on St. Ignace Island was found to be one of the best winter ranges on the island. Comparison of this area with the total study area indicates that the more nearly equal availability of several food species constitutes an important feature which attracted moose into this valley. This seems to substantiate other general observations which indicate that moose prefer areas providing the greatest variety of available food. The age composition of the several food species in Otter Creek Valley compared to the entire study area provides an important index to the production of favourable moose habitat. The high occurrence of shrubs and saplings in this area as compared to the whole island indicates that an assessment of the age composition of the principal food species of an area should give reliable criteria for evaluating its potentialities as a moose producing habitat.

A well defined winter "yard" was studied in Algonquin Provincial Park, Ontario, in which the extent of area seemed to be closely correlated with the local distribution of balsam fir.

Forest fires are apparently one of the most important agents affecting forest succession. In many localities, old burned-over areas are producing the majority of available food during all seasons except perhaps during the summer months. Two small areas, burned over in 1936, were studied. At present these areas are providing a significant proportion of the available

white birch, willow and quaking aspen in the St. Ignace area. The size of a burned-over area appears to show a direct relationship to its degree of utilization by moose. Preliminary investigations suggest that large burned-over tracts do not normally become heavily populated until a balanced winter and summer habitat becomes available. Key factors under such circumstances in the eastern part of the moose range seem to be (1) sufficient variety of foods for all seasons including (2) aquatic vegetation in summer and (3) balsam fir in winter.

Preliminary investigations suggest that the effect of lumbering operations on the habitat of moose is dependent on the types of lumbering operations practised. Clean cutting of vast areas appears to reduce maximum utilization for a certain period. Selective cutting, on the other hand, frequently fails to reduce the forest canopy sufficiently to allow successional growth. The physical operations of lumbering apparently have little detrimental effect on moose unless wilful disturbance or shooting of the animals is carried out. Under most circumstances the clean cutting of small spots or strips apparently will normally increase the available food supply and thereby improve the habitat for moose. The relationships of moose and other types of lumbering operations depend on many local conditions.

Forest insects, especially the spruce budworm, constitute important factors in the general ecology of moose. The complex role of forest insects in various biotic communities, in terms of their effect on such forms as moose and deer, is as yet poorly understood. In the case of the spruce budworm serious local destruction of balsam fir has greatly reduced the available supply of this important winter food of moose.

Preliminary studies of the effect of moose on the habitat indicate that these animals become an important factor in the development of a forest community. In areas where an apparent balance of the moose population with a carrying capacity of the habitat exists, moose tend to help maintain or improve their own habitat conditions. In areas of extremely low populations the habitat usually matures or passes through normal successional stages to become less favourable for moose, while in over-populated areas moose may tend to suppress regeneration of important moose foods which in turn may also result in less favourable habitat conditions.

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